

Spatial modeling of Bering Sea walleye pollock with integrated age-structured assessment models in a changing environment

Peter-John F. Hulson, Terrance J. Quinn II, Dana H. Hanselman, and James N. Ianelli

Abstract: Climate change may affect the spatial distribution of fish populations in ways that would affect the accuracy of spatially aggregated age-structured assessment models. To evaluate such scenarios, spatially aggregated models were compared with spatially explicit models using simulations. These scenarios were based on hypothetical climate-driven distribution shifts and reductions in mean recruitment of walleye pollock (*Gadus chalcogrammus*) in the eastern Bering Sea. Results indicate that biomass estimates were reasonably accurate for both types of estimation models and precision improved with the inclusion of tagging data. Bias in some aggregated model scenarios could be attributed to unaccounted-for process errors in annual fishing mortality rates and was reduced when estimating effective sample size or time-varying selectivity. Spatially explicit models that allow estimation of variability in movement and ontogenetic parameters (specified as a random walk process) were shown to be feasible, whereas models that misspecified ontogenetic movement and climate change effects resulted in biased biomass and movement parameter estimates. These results illustrate that more complex models may characterize processes better but may be less robust for management advice.

Résumé : L'effet des changements climatiques sur la répartition spatiale de populations de poissons peut avoir une incidence sur l'exactitude des modèles d'évaluation des stocks structurés par âge spatialement agrégés. Pour évaluer de tels scénarios, des modèles spatialement agrégés ont été comparés à des modèles spatialement explicites à l'aide de simulations. Ces scénarios sont basés sur des phénomènes hypothétiques d'origine climatique de modification de la répartition et de diminution du recrutement moyen des goberges de l'Alaska (*Gadus chalcogrammus*) dans la mer de Behring orientale. Les résultats indiquent une exactitude raisonnable des estimations de la biomasse issues des deux types de modèles d'estimation et une augmentation de la précision associée à l'intégration de données de marquage. Des biais associés à certains scénarios de modèle agrégé peuvent être attribués à des erreurs de traitement dans les taux annuels de mortalité par pêche n'ayant pas été prises en considération. Ces biais ont pu être réduits pour l'estimation de la taille d'échantillon effective et de la sélectivité variable dans le temps. La faisabilité de modèles spatialement explicites qui permettent d'estimer la variabilité des déplacements et de paramètres ontogénétiques (définis selon un processus de cheminement aléatoire) est également démontrée, alors que des modèles caractérisés par une définition erronée des déplacements ontogénétiques et des effets des changements climatiques ont donné des estimations biaisées de la biomasse et des paramètres de déplacement. Ces résultats illustrent le fait que, si des modèles plus complexes peuvent fournir une meilleure caractérisation des processus, ces modèles peuvent toutefois s'avérer moins robustes pour ce qui est d'éclairer la gestion des stocks. [Traduit par la Rédaction]

Introduction

Spatial modeling of fish stocks for the purposes of fishery management is relatively uncommon, with notable exceptions including tunas (e.g., Hampton and Fournier 2001), school shark (Punt et al. 2000), and rock lobster (McGarvey et al. 2010). With spatially disaggregated datasets and mark-recapture information, spatially explicit models can be developed that estimate movement between regions (Goethel et al. 2011). The primary limitation to implement spatial models is the lack of resolution in the available spatially disaggregated datasets. Consequently, stock assessment scientists will construct models that typically cover broad geographic scales and implicitly assume that spatial heterogeneity of fish populations roughly coincides with fishery patterns.

Spatially explicit accounting for fish populations is also an important step in moving towards ecosystem-based fisheries management (Quinn and Collie 2005; Marasco et al. 2007; Goethel et al. 2011). To make ecosystem-based fisheries management opera-

tional, a spatially explicit model allows for interactions among aquatic species at finer spatial scales, as modeling at broad geographic scales may miss important population processes (Härkönen and Harding 2001). Further, spatially explicit stock assessment models contribute to understanding the interactions between fish and environmental influences within geographically distinct habitats (Mueter et al. 2006). For these reasons, the demand for advances in implementing spatial components within stock assessment models has increased.

Research conducted by the Intergovernmental Panel on Climate Change (IPCC) has found that global mean temperatures are rising (Intergovernmental Panel on Climate Change 2007), which could have an influence on the spatial distribution of fish species evaluated with fisheries stock assessment models (Mueter and Litzow 2008). Thus, the potential effects of climate change on the spatial distribution of fish populations need to be identified (Beamish et al. 2004). A primary effect of climate on the distribution

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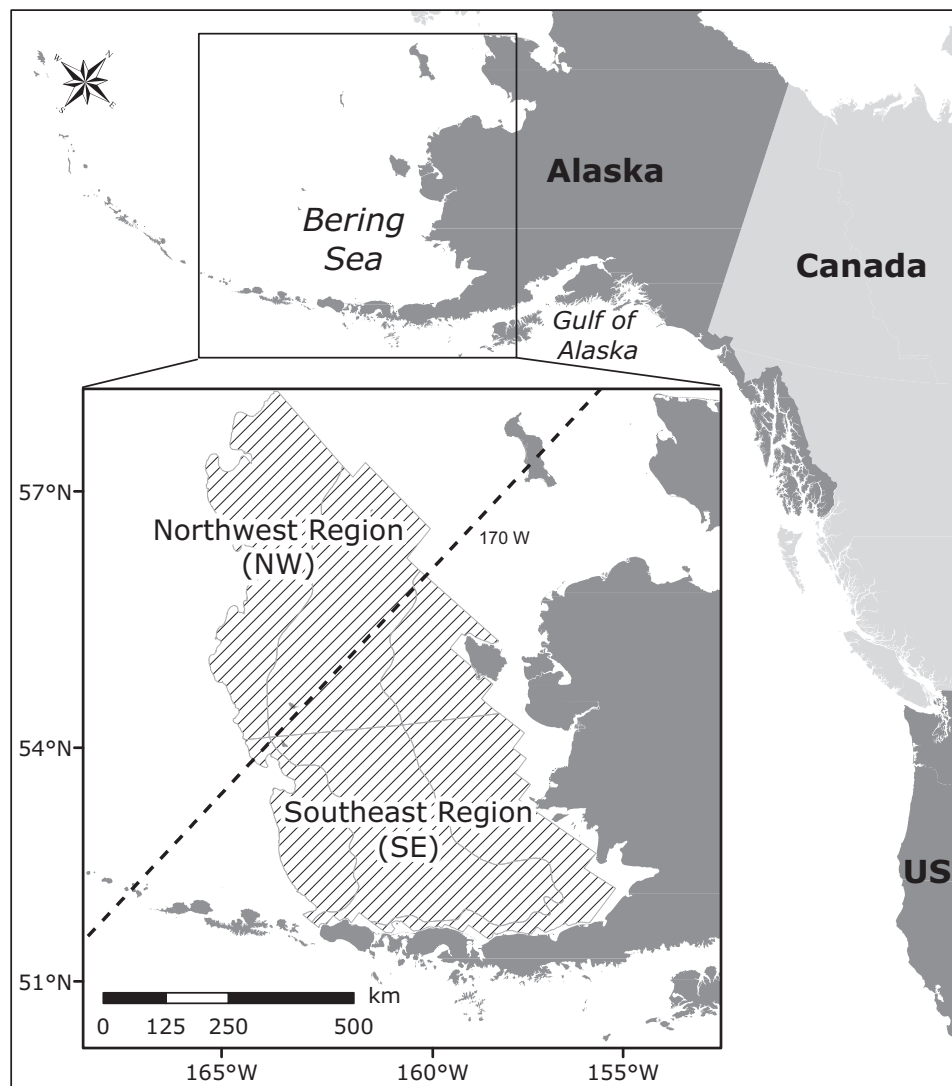
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Fig. 1. Map showing the northwest and southeast regions of the eastern Bering Sea considered in the spatial modeling of walleye pollock.



of fish in the Northern Hemisphere is hypothesized to manifest as a northward shift (Perry et al. 2005; Cheung et al. 2009). A number of studies have examined the ecological implications of climate change through simulation (Hashioka and Yamanaka 2007; Munday et al. 2008; Ianelli et al. 2011a), but the performance of fisheries stock assessment models when applied to fish populations influenced by climate change has not been investigated. Also, the accuracy and precision of spatially aggregated stock assessment models used to manage fisheries should be evaluated when considering climate change.

A spatially explicit stock assessment model from Miller et al. (2008) and Hulson et al. (2011) for eastern Bering Sea (EBS) walleye pollock (*Gadus chalcogrammus*, hereafter referred to as “pollock”) is used in this study, as it provides an excellent example of a fish species that could be affected by climate change (Overpeck et al. 1997). The spatially explicit model for EBS pollock includes two regions, the northwest and southeast, divided by the 170°W meridian, and two commercial fishery seasons (A: winter–spring season; B: summer–fall season; Fig. 1; Miller et al. 2008). In the spatially explicit age-structured assessment (ASA) model, movement between regions was assumed to occur after each season between the spawning and feeding grounds. Further details, including parameters estimated and population dynamics equations in the spatially explicit ASA model, can be found in Miller et al. (2008)

and Hulson et al. (2011). The latter group of authors performed simulation testing without climate change effects and found that the spatially explicit model was accurate and precise, especially when mark-recapture data were available.

Owing to potential warming in the southern latitudes, a northward latitudinal shift would result in an increase in EBS pollock abundance in the northwest region and a decrease in the southeast region (e.g., Perry et al. 2005). In the EBS, pollock distribution and, by inference, movement have been shown to be correlated with temperature (Kotwicki et al. 2005). Further, EBS pollock recruitment has been found to be inversely related to temperature, so recruitment could decrease with increased temperatures in the EBS, as forecasted by the IPCC climate models (Mueter et al. 2011). In this study we tested the effects of a hypothetical northward shift and a decrease in mean recruitment in the EBS pollock population resulting from increasing temperatures due to climate change. Through simulation, our goal was to investigate the accuracy and precision of spatially aggregated models compared with spatially explicit models used to assess a population whose spatial distribution is affected by climate change.

Materials and methods

To compare between spatially aggregated and spatially explicit models under different movement and recruitment scenarios

that were impacted by climate change, we followed a four-step process in this simulation analysis. In the first step, spatially explicit operating model cases were constructed with “known” population structure (Table 1). Within the operating model, different types of movement were considered, including no movement, random movement, and climate change influences on movement. Hypothetical effects of climate change on movement and recruitment were considered by shifting the population of EBS pollock to the north and reducing the mean recruitment (e.g., Cheung et al. 2009; Mueter et al. 2011).

In the second step, datasets that can be integrated into ASA models (e.g., catch, population index, age composition, and tag recoveries) were taken from the operating model cases and error was generated. The simulated datasets were generated assuming statistical distributions about observations (e.g., sampling error) and processes (e.g., recruitment variability). In the third step, estimation models were constructed as either spatially explicit or spatially aggregated forms of ASA models. Different estimation model scenarios were then applied to the generated datasets from the first and second steps (Table 1). The spatially explicit form estimated movement between regions, while the spatially aggregated form combined the regional data and modeled the entire population in the EBS. In the fourth and final step, estimation model performance was evaluated through bias and uncertainty compared with the “known” population quantities from the operating model cases. In the following sections, further details of each of the four steps taken in this study are provided. Additional details, including further description of operating and estimation model structures, parameters used in the operating model, and climate change influences on movement and recruitment are provided in the online supplementary material¹.

Operating model

The operating model used in the first step of this simulation analysis was based on a two-region and two-season spatially explicit ASA model for EBS pollock (Miller et al. 2008). The spatially explicit ASA model used in Miller et al. (2008) was fit to regionally disaggregated datasets and estimated parameters for regional recruitment, regional initial abundance, regional and seasonal fishing mortality, fishery and survey selectivity, survey catchability, and movement parameters. The estimated parameters and model structure from Miller et al. (2008) were used in this study to construct the operating model.

In the operating model there were two periods of movement. In the first, fish moved from the spawning to summer feeding grounds after the A season. After the B season, fish moved from the summer feeding grounds back to the spawning grounds in the second period of movement. Movement of EBS pollock has been found to be related to age (Buckley et al. 2001), and this relationship was accounted for in several cases of the spatially explicit operating model. In the cases that considered ontogenetic movement, the proportion of fish that remained in the northwest region was specified as a decreasing function of age for both the A and B fishing seasons. The proportion of fish specified to remain in the southeast region after the A and B seasons was constant across ages based on available knowledge.

In the operating model, as in Miller et al. (2008) and Hulson et al. (2011), the probability that a fish stayed in the same region ($R \rightarrow R P_S$) was estimated as the inverse-logit function

$$(1) \quad R \rightarrow R P_S = \frac{1}{e^{-\theta_{R,S}} + 1}$$

Table 1. Notation and description of the operating model cases and estimation model scenarios evaluated.

Notation	Description
Operating model cases	
O0	No movement between regions, time- and season-dependent F equal among regions (averaged across regions from Miller et al. (2008) and Hulson et al. (2011))
O1	Random movement among regions, time-, season-, and region-dependent F same as that in Miller et al. (2008) and Hulson et al. (2011)
O2	Movement and F same as that in Miller et al. (2008) and Hulson et al. (2011); no climate change influence
O3	Movement and F same as that in Miller et al. (2008) and Hulson et al. (2011); moderate climate change over final 15 years
O4	Movement and F same as that in Miller et al. (2008) and Hulson et al. (2011); extreme climate change over final 15 years
Estimation model scenarios	
Spatially aggregated ASA model	
A1	Logistic time-invariant fishery selectivity, multinomial age composition likelihood, no tagging data
A2	Logistic time-invariant fishery selectivity, Dirichlet age composition likelihood, no tagging data
A3a	Nonparametric time-varying selectivity, multinomial age composition likelihood, no tagging data
A3b	Nonparametric time-varying selectivity, multinomial age composition likelihood, include tagging data
Spatially explicit ASA model	
E0a	Ontogenetic and climate change parameters and functional form known, no tagging data
E0b	Ontogenetic and climate change parameters and functional form known, tagging data included
E1	Ontogenetic parameters misspecified, climate change parameters and functional form known, tagging data included
E2	Climate change parameters misspecified, ontogenetic parameters and functional form known, tagging data included
E3	Climate change and ontogenetic parameters estimated, functional form known, tagging data included
E4	Climate change and ontogenetic parameters estimated with random walk, functional form unknown, tagging data included

where $\theta_{R,S}$ are the logit-transformed region (R) and fishing season (S) specific movement parameters. Ontogenetic movement in the northwest region was constructed in the operating model as a linear function of age. The probability that fish stayed in the northwest region for ages 4–10+ was given by

$$(2) \quad {}^{NW \rightarrow NW}P_{a+1,S} = {}^{NW \rightarrow NW}P_{a,S} {}^{NW}Q_S$$

where ${}^{NW}Q_S$ is a proportion that decreased the retention of fish in the northwest (NW) region by age (a) in season S . Similar to the movement probabilities, ${}^{NW}Q_S$ was estimated as the inverse-logit function:

$$(3) \quad {}^{NW}Q_S = \frac{1}{e^{-\gamma_{NW,S}} + 1}$$

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0020>.

where $\gamma_{NW,S}$ is the logit-transformed ontogenetic parameter for the northwest region in season S .

Recruitment in the operating model was defined as the number of age-3 fish (in millions) and was parameterized as in Miller et al. (2008) and Hulson et al. (2011). Region-specific recruitment for age-3 was estimated with a mean recruitment parameter (\bar{N}_3), a scalar allocating the fraction of recruitment between regions (ϕ), and annual deviations in recruitment (δ_y^R). Recruitment for the northwest and southeast regions was given by

$$(4) \quad \begin{aligned} {}_{NW}N_{3,y} &= (1 - \phi) \times \bar{N}_3 \times e^{\delta_y^{NW}} \\ {}_{SE}N_{3,y} &= \phi \times \bar{N}_3 \times e^{\delta_y^{SE}} \end{aligned}$$

where ${}_{NW}N_{3,y}$ is recruitment in the northwest region, and ${}_{SE}N_{3,y}$ is recruitment in the southeast region.

Operating model cases were configured to evaluate spatially aggregated and spatially explicit model performance by including varying degrees of movement and mean recruitment, which in some cases was affected by climate change (Table 1). Movement in the operating model cases included no movement, random movement, and movement following Miller et al. (2008). Further operating model cases were considered in which climate change effects on movement resulted in a shift in the distribution of pollock in the EBS to the northwest region. Climate change effects on recruitment involved a decrease in the overall mean recruitment.

Operating model case O0 was constructed as a spatially static population with no movement between regions (i.e., the probability of staying in region R was set to 1), and the fully recruited annual fishing mortalities within seasons A and B were equal across regions (set at the mean annual fishing mortality between the northwest and southeast regions). Operating model O1 was constructed with random movement between regions across ages and years (generated with the uniform distribution, illustrated for the probability of staying in the northwest region after the A season in the online supplementary material) and fully recruited annual fishing mortalities that were unequal across regions, as in Miller et al. (2008) and Hulson et al. (2011). Operating model case O2 was the same as used in Miller et al. (2008) and Hulson et al. (2011), for which the parameter estimates and model structure are provided in the supplementary material section. Operating model cases O3 and O4 were constructed to evaluate climate change influences on movement and mean recruitment. The period over which climate change occurred was specified as occurring for the final 15 years of the operating model.

We are unaware of any literature that provides functional relationships between climate change and movement parameters in fish populations. The literature that does exist on the relationship between movement and climate change (i.e., Perry et al. 2005; Cheung et al. 2009) hypothesizes that a northward shift of distribution to suitable habitat could occur, but these studies fail to provide any functional relationships. For simplicity, time-dependent changes in movement parameters within the operating model were constructed with linear functions. These functions were applied to the logit-transformed movement parameters to be consistent with the models in Miller et al. (2008), who also used the logit transformation.

The shift in the EBS pollock distribution to the northwest region was produced in the operating model through a linear function of the logit-transformed movement parameters given by

$$(5) \quad \theta_{R,S,y+1} = \theta_{R,S,y} \times \kappa_\theta$$

where κ_θ is the climate change parameter for movement, and $\theta_{R,S}$ are the logit-transformed region (R) and fishing season (S)

specific movement parameters used to estimate the probability that fish stayed in the same region ($R \rightarrow RP_S$; eq. 1). Like the movement parameters, logit-transformed ontogenetic age-dependent movement was also specified as a function of κ_θ to give increased retention in the northwest region with increasing age by

$$(6) \quad \gamma_{NW,S,y+1} = \gamma_{NW,S,y} \times \kappa_\theta$$

where $\gamma_{NW,S}$ is the logit-transformed ontogenetic parameter for the northwest region in season S to estimate the proportion that decreased the retention of fish in the northwest region by age (${}^{NW}Q_S$; eq. 3).

To reflect possible climate impacts on the distribution of regional biomass for the climate change cases, κ_θ was set at 1.07 in operating model case O3 and 1.2 in operating model case O4. The climate change parameter applied to the logit-transformed movement and ontogenetic parameters thus increased retention in the northwest region over time and with age. An illustration of how the climate change parameter κ_θ affected movement over time and age for operating model cases O2–O3 is shown in the online supplementary material for the probability of staying in the northwest region after the B season (${}^{NW \rightarrow NW}P_{a,y,B}$).

Mueter et al. (2011) found that with increased temperatures in the EBS, mean pollock recruitment decreased. Thus, with potential climate change effects that increase the temperature of the EBS in operating model cases O3 and O4, we also decreased mean recruitment in these cases. Similar to the linear function for the movement parameters, mean recruitment was decreased in the operating model with a linear function applied to the log-transformed mean recruitment parameter ($\ln \bar{N}_3$) given by

$$(7) \quad \ln \bar{N}_{3,y+1} = \ln \bar{N}_{3,y} \times \kappa_{\bar{N}_3}$$

where $\kappa_{\bar{N}_3}$ is the climate change parameter applied to the log-transformed mean recruitment parameter.

To produce a decrease in mean recruitment due to warming temperatures in operating model cases O3 and O4, the parameter $\kappa_{\bar{N}_3}$ was selected so that the untransformed mean total recruitment decreased. Mueter et al. (2011) found that mean recruitment under climate change could decrease by 1% per year. In operating model case O3, $\kappa_{\bar{N}_3}$ was set at 0.996, which resulted in a 7.5% decrease in mean recruitment over the final 15 years of the operating model compared with the case in which there was no climate change effect on movement or recruitment (i.e., half of the value that resulted from Mueter et al. 2011). In operating model case O4, $\kappa_{\bar{N}_3}$ was set at 0.99, resulting in a 15% decrease in mean recruitment over the final 15 years of the operating model, which follows the predictions of Mueter et al. (2011). Annual deviations in recruitment were held constant between operating models to avoid spurious trends in mean recruitment beyond that driven by climate change. The total, northwest, and southeast recruitment across the time series of the operating model for cases O0–O4 and the mean recruitment across the final 15 years are shown in the online supplementary material.

Data generation

In the second step of the simulation analysis, error was generated in datasets drawn from the operating model cases. The datasets that were generated included catch biomass (regional, seasonal, and total), population abundance indices (from surveys), age composition (both for catch and surveys), and tag recovery data. The time series for each of the datasets followed from the spatially explicit model used in Miller et al. (2008). Datasets used in the original spatially explicit ASA model from Miller et al. (2008) that was used to construct the operating model in this study ranged from 1977 to 2005 and included ages 3–10+ in the age

composition. Commercial fishery data included total fishery yield for all years from 1977 to 2005, fishery yield from the northwest region for the A season (1977–1987, 1991–1996, and 1998–2004) and B season (1977–1987, 1991–2004), and fishery yield from the southeast region for the A and B seasons (both for years 1977–1987, 1991–2004). Fishery-independent indices of abundance included the Alaska Fisheries Science Center (AFSC) bottom trawl survey (BTS) biomass estimates from 1982 to 2004 and the AFSC echo-integration trawl (EIT) survey in the years 1994, 1996–1997, 1999–2000, and 2002. Age composition data were included for each year of the regional and seasonal commercial fishery catch, BTS, and EIT. A hypothetical tagging program was implemented in the operating model and followed the approach in [Hulson et al. \(2011\)](#). One main difference between the current study and [Hulson et al. \(2011\)](#) was that the simulated tags were released for the last 10 years of the time series rather than the last 3 years.

Error in catch and index data for the commercial fishery, BTS, and EIT was generated using the log-normal distribution. Commercial fishery yield in the northwest and southeast regions for the A and B fishing seasons were generated with a standard deviation (SD) of 0.05, and regional BTS and EIT biomass datasets were generated with a SD of 0.2 following [Hulson et al. \(2011\)](#). Spatially aggregated index data were obtained by summing the untransformed generated regional index data. To compute the distribution of the sum of untransformed log-normal random variables the Fenton and Wilkinson approximation method was used ([Gao et al. 2009](#)). This method provided approximate SDs with means over time of 0.14, 0.15 for the EIT biomass, 0.04 for the A and B season catch biomass, and for the total catch biomass a mean SD of 0.03.

Age composition datasets for the commercial fishery, BTS, and EIT were generated assuming the multinomial distributions. For each year of the regional and seasonal fishery age composition, regional BTS age composition, and regional EIT age composition, multinomial error was generated based on the age composition from the operating model and an assumed sample size of 200. The sample size of 200 is far smaller than the actual sample sizes collected for EBS pollock but represents the approximate level of overdispersion and uncertainty in the age composition (e.g., [McAllister and Ianelli 1997](#)). The spatially aggregated age composition was obtained by summing the generated multinomial samples from the regional age compositions.

Recovery tagging data were generated with the Poisson distribution. Following previous research into the feasibility of tagging EBS pollock, 10 000 tags were released in the simulation during the BTS ([Miller 2007](#)). In [Hulson et al. \(2011\)](#) it was found that uncertainty was reduced when releasing tags evenly across the two regions. Thus, in this study tags were released uniformly by age and region. In this case, tagging uniformly across ages mimics a length-stratified sampling design in which the same number of tags would be released across length bins. For simplicity, the numbers of tags released by age were assumed known. Tag recoveries occurred during fishing and were generated with the Poisson distribution. The proportion of total catch that was examined for tags was set at 7% for the northwest region and 39% for the southeast region and was based on the proportion of catch that was landed to shoreside processors ([Miller 2007](#)). Thus, the generated total number of tags caught in the commercial fishery was multiplied by the proportion of catch delivered to shoreside processors in each region to obtain the tag recovery datasets.

For each operating model case, catch biomass, survey index, age composition, and tag recovery datasets were generated 1000 times ([Efron and Tibshirani 1993](#)) using R ([R Development Core Team 2008](#)).

Estimation models

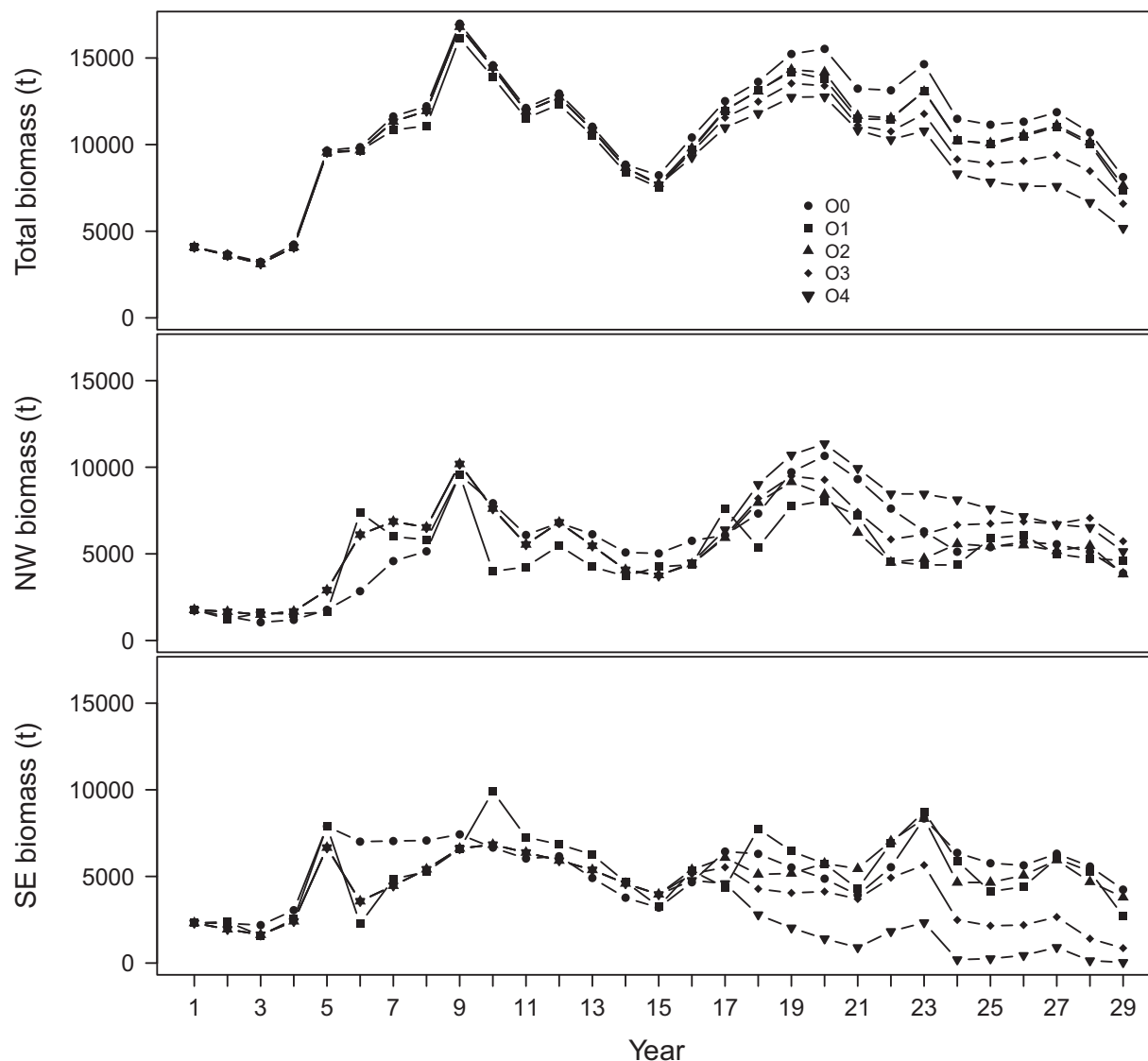
In the third step of the simulation analysis, estimation model scenarios were constructed that integrated the datasets generated

in the second step. We evaluated two estimation models in this study: a spatially aggregated ASA model and a spatially explicit ASA model. In total there were 10 estimation model scenarios considered in this study; four for the spatially aggregated ASA model and six for the spatially explicit ASA model (notation and description of estimation model scenarios is provided in [Table 1](#)). The spatially aggregated model is similar in structure to the current ASA model used to manage EBS pollock ([Ianelli et al. 2011b](#)). The spatially aggregated model used in this study and the current assessment model both model the EBS pollock population as a whole, rather than regionally disaggregated datasets. The primary differences between the spatially aggregated estimation model used in this study and the current assessment used for EBS pollock are in the time-dependent parameterizations of parameters. The spatially explicit model integrated tagging data as in [Hulson et al. \(2011\)](#) and was based on the Integrated Tagging and Catch-at-Age Analysis (ITCAAN) model after [Maunder \(2001\)](#) and estimated movement between the northwest and southeast regions of the EBS.

Fundamentally, the spatially aggregated and spatially explicit models are the same; both use the same underlying theory to describe the population dynamics and the same statistical distributions to fit the datasets. The only difference between the models is the expansion of the population dynamics to include movement estimation in the spatially explicit model by estimating movement parameters that are supported through the use of spatially disaggregated datasets and tagging data. In the spatially aggregated and spatially explicit models, the half-year time steps are the same, and fishing mortality and half of natural mortality are applied after the A and B fishing seasons (winter and summer). The difference between the spatially aggregated and spatially explicit models in this regard is that movement occurs in the spatially explicit model coincident with the half-year time steps. Both the spatially aggregated and spatially explicit ASA estimation models used the log-normal distribution for index and catch biomass datasets, the multinomial distribution for the age composition datasets, and the Poisson distribution for the tag recovery datasets to obtain the maximum likelihood estimates of the estimated parameters.

Four estimation model scenarios were evaluated with the spatially aggregated model (A1–A3b, where “A” stands for spatially aggregated in the notation of estimation model scenarios; [Table 1](#)). Within the spatially aggregated estimation model scenarios we tested the treatment of the age composition likelihood (A1 and A2), the treatment of time-dependent fishing selectivity (A3a and A3b), and the inclusion of spatially aggregated tagging data (A3a and A3b, where “a” denotes not including tagging data and “b” denotes including tagging data).

Six estimation model scenarios were evaluated with the spatially explicit ASA (E0a–E4, where “E” stands for spatially explicit in the notation of estimation model scenarios; [Table 1](#)). With these model scenarios we tested the inclusion of spatially disaggregated tagging data (E0a and E0b); the misspecification of ontogenetic (age-dependent) or climate change (time-dependent) influences on movement (E1 and E2, in which we defined misspecified as constant and set at 1 over age or time when it varies in the operating model); estimating rather than setting ontogenetic and climate change parameters with the functional form known (E3); and estimating age- and time-dependent movement with a random walk (E4; e.g., as in [Wilberg and Bence 2006](#)). To reduce the number of parameters for such random walk processes under estimation model scenario E4, we assumed that the relative annual changes in the parameters would have a similar relationship with climate change. We applied a single time series of annual deviations to the regional and seasonal movement parameters and ontogenetic parameters with a scaled random walk, given by

Fig. 2. Total, northwest (NW), and southeast (SE) biomass (t) for operating model cases O0–O4.

$$(8) \quad \theta_{R,S,y+1} = \theta_{R,S,y} + \delta_y \times \theta_{R,S,y=0}$$

where $\theta_{R,S,y}$ was the logit-transformed movement parameter, δ_y was the shared annual estimated deviation in movement, and $\theta_{R,S,y=0}$ was the initial movement parameter estimate.

Model performance

In the fourth and final step of this analysis, results from the estimation model scenarios were compared to the “known” population structure from the operating model cases. Estimation model performance among the scenarios focused on representing bias and uncertainty in biomass (both total and regional) in the final year and estimated movement and ontogenetic parameters (for the spatially explicit estimation models). For brevity of results, biomass in the last year of the model was selected for presentation rather than the full time series, because it is the most critical year from which forecasts and harvest recommendations are used for management. The root mean squared error (RMSE) for these outputs was presented to quantify both bias and uncertainty. Boxplots were used to show estimation results from the simulated operating model scenarios. These readily allow comparisons of median, interquartile ranges, and 95th percentiles.

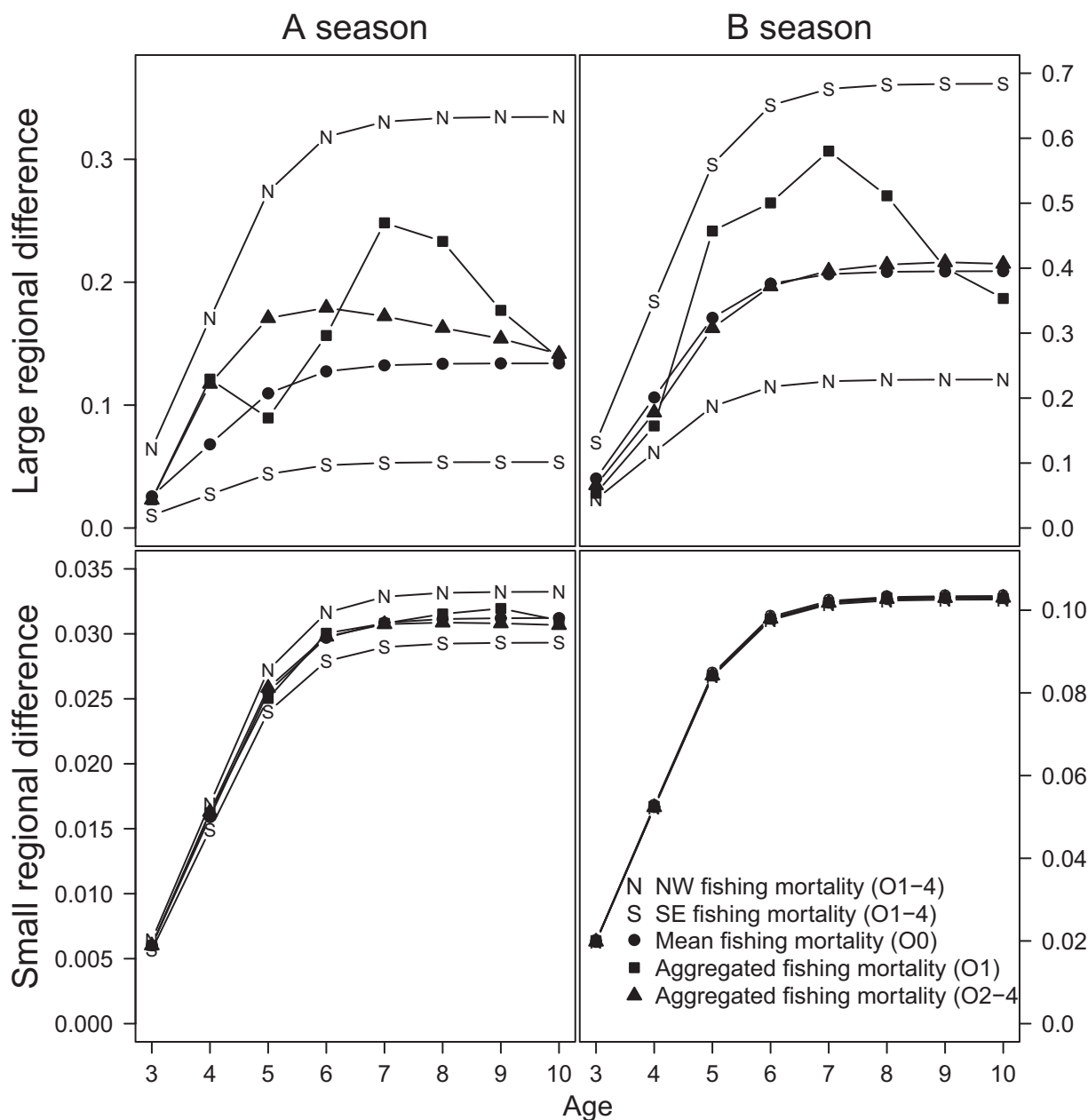
Estimates were considered significantly biased if the “true” operating model value fell outside the 95th percentiles from the estimation model.

Some estimation model scenario and operating model combinations were omitted from presentation. For operating model case O0 (static spatial population), estimation model scenarios E1 and E2 were equivalent to E0. Similarly, estimation models scenarios E0a, E0b, and E2 were omitted for operating model case O1 because the functional forms of ontogenetic movement or climate change influences were absent. Finally, operating model case O2 estimation model scenario E2 was omitted because climate change influences in this operating model case were absent.

Results

The total biomass of EBS pollock were similar for operating model cases O0–O2 and decreased in operating model cases O3 and O4 at the end of the time series as the number of years increased in which climate change affected movement and recruitment (top panel, Fig. 2). The spatial distribution of biomass in the operating model resulted in a small increase in biomass in the northwest region (middle panel, Fig. 2) and a large decrease in biomass in the southeast region (bottom panel, Fig. 2) in operating

Fig. 3. A and B season fishing mortality at age from the operating model cases for years with large and small differences between the northwest (NW) and southeast (SE) regional fishing mortality.

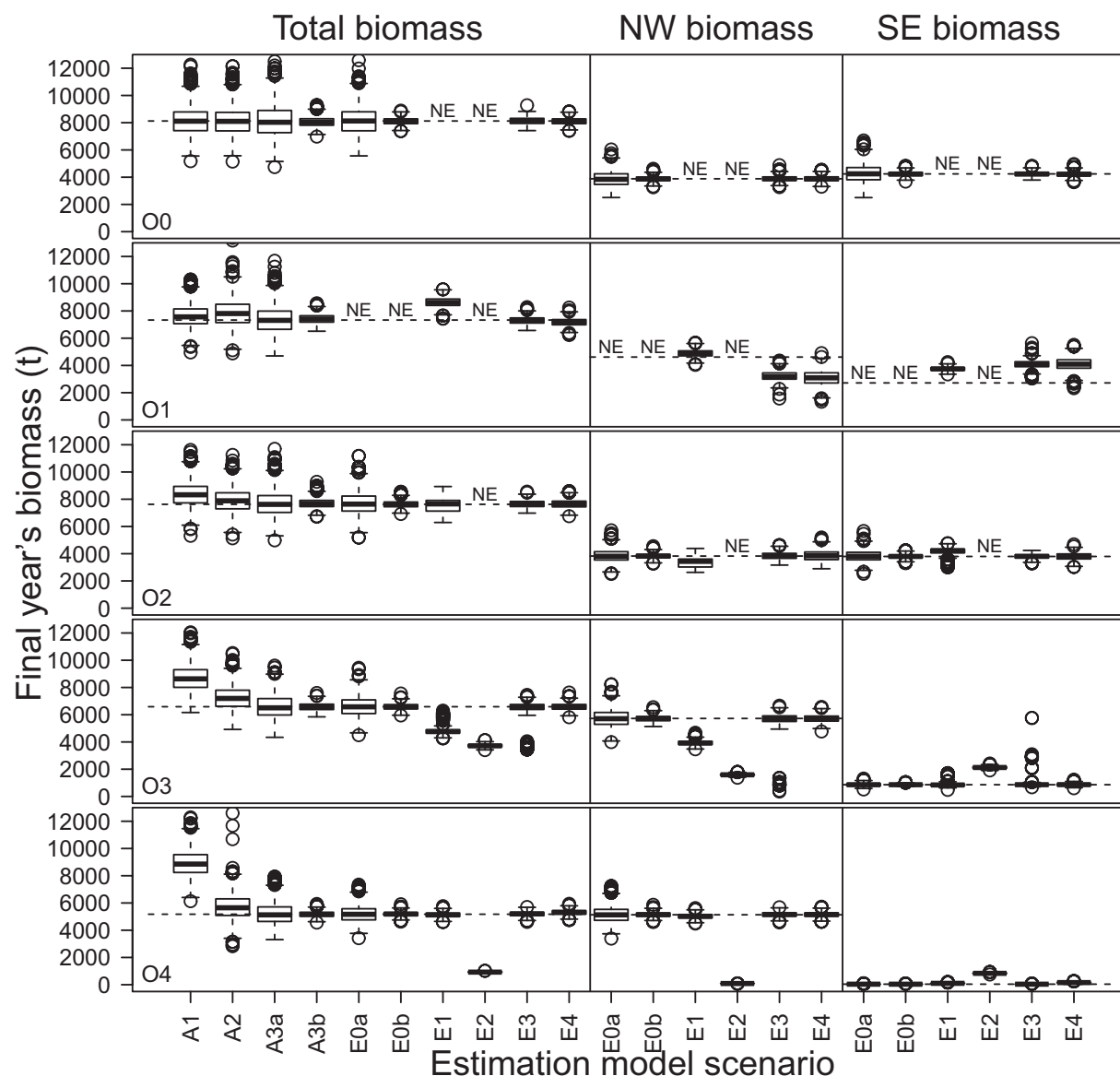


model cases O3 and O4 compared with operating model cases O0–O2. The shift of biomass from the southeast to northwest regions of the EBS in operating model cases O3 and O4 represent cases across a continuum of possible climate effects on spatial distribution, one extreme (O4) and one more moderate (O3). While the extreme case (O4) may shift distribution abruptly, these cases were considered to evaluate both spatially aggregated and spatially explicit model performance under different levels of climate change impacts. An interesting result of the operating model was that spatially summed fishing mortality at age showed a dome-shaped pattern for operating model cases O1–O4 (Fig. 3, top panels). Alternatively, when regional differences in fishing mortality at age were small, the aggregated fishing mortality at age was asymptotic and similar to the regional fishing mortalities (Fig. 3, bottom panels).

In general, most of the estimation models resulted in unbiased estimates of total biomass in the final year across the operating

model cases (Fig. 4). The exceptions in which bias in the final year's total biomass occurred was estimation model scenario E1 in case O1, estimation model scenarios E1 and E2 in case O3, and estimation model scenario E2 in case O4. Bias in regional biomass occurred for estimation model scenarios E1, E3, and E4 in case O1, estimation model scenarios E1 and E2 in case O3, and estimation model scenario E2 in case O4. Total biomass estimates from estimation model scenarios A1 and A2 were unbiased across the operating model cases (with the exception of case O4). However, there were differences when comparing the median value from estimation model scenarios A1 and A2 to the true value from the operating model in cases O2–O4. The positive difference in estimation model scenarios A1 and A2 became larger as the magnitude of climate change increased. The difference between the median and true value was smaller for estimation model scenario A2 compared with A1 for all operating model cases.

Fig. 4. Total and regional biomass estimated in the final year from the estimation model scenarios. The horizontal dashed lines are the true values from the operating model, and “NE” stands for estimation model scenarios that were not estimated in the specific operating model case.



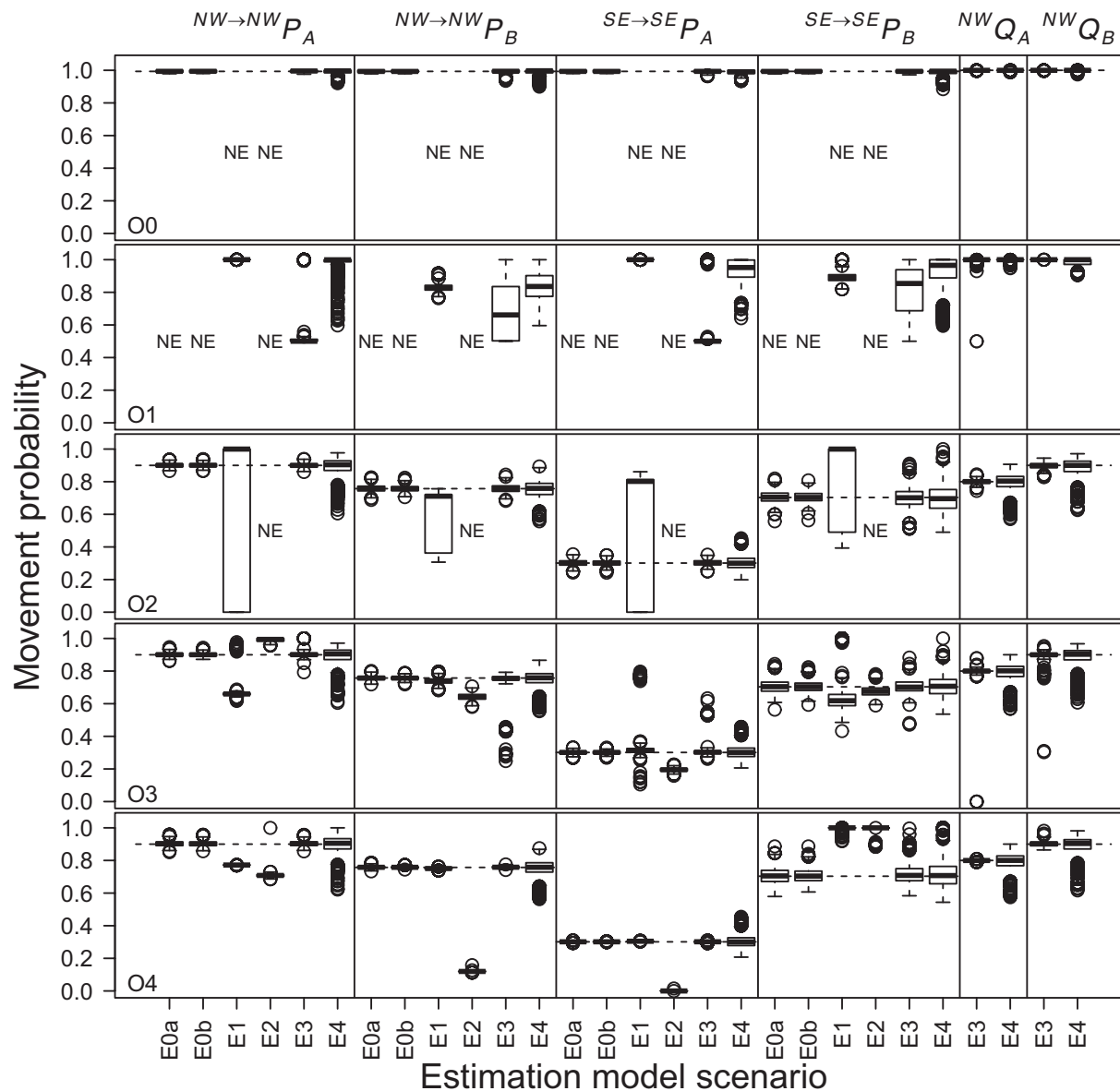
When bias resulted in the final year's biomass for operating model cases O3 and O4 from the spatially explicit model scenarios, bias also resulted in the estimated probability of movement (Fig. 5). Additionally, bias in the probability of movement occurred for scenario E1 in case O4, even though bias did not occur in the final year's biomass. The estimated probability of movement resulted in large uncertainty for scenario E1 in case O2, in some cases ranging from 0 to 1, or nearly so. For case O1, in which movement between regions was random, the estimated probability of movement was either 1 with low uncertainty or not equal to 1 with large uncertainty. For scenarios E3 and E4, the probability of movement by age ($P^{NW}_{Q_5}$) for both the A and B seasons was unbiased for operating model cases O0 and O2–O3. Further, the time-dependent movement and ontogenetic parameter estimates were unbiased for the scaled random walk estimation model scenario E4 (Fig. 6; probability of staying in the northwest region after the B season is shown as an example).

For all operating model cases the largest RMSE in total and regional biomass in the final year resulted from the estimation

model scenarios that did not include tagging data and scenarios that resulted in bias (Fig. 7). Estimation models that included tagging data and were unbiased in the final year's biomass resulted in small RMSE of similar magnitude. For example, across the operating model cases the RMSE in the final year's biomass for estimation model scenario A3b was similar to scenarios E0b–E4 (with the exception of scenarios E0b–E4 that resulted in bias). Alternatively, the magnitude of RMSE in the final year's biomass was similar for estimation models without tagging data. When comparing between model scenarios A3a and E0a, and A3b and E0b, for all of the operating model cases the RMSE in the final year's biomass was smaller for the spatially explicit model scenario (E0a and E0b) compared with the spatially aggregated model scenario (A3a and A3b).

When tagging data were included in the estimation model scenarios the uncertainty in the fishing mortality parameters and survey catchability parameters decreased (Figs. 8 and 9). For all operating model cases, the coefficient of variation (CV) in fishing mortality for scenarios A3b and E0b was smaller than scenar-

Fig. 5. Probability of staying in region R and season S ($R \rightarrow R P_S$) and probability of ontogenetic movement ($NW Q_S$) estimated by the spatially explicit estimation model scenarios. The horizontal dashed lines are the true values from the operating model (omitted for case O1, as movement was random), and “NE” stands for estimation model scenarios that were not estimated in the specific operating model case.



ios A3a and E0a (Fig. 8, shown for operating model case O0 as an example). For both scenarios A3b and E0b, the CVs for the fishing mortality parameters were similar to those from A3a and E0a at the beginning of the time series, but became smaller later in the time series. Additionally, the CVs in the survey catchability parameters (both BTS and EIT) decreased when tagging data were included in the estimation model scenarios. Across operating model cases O0–O4, the CV in catchability from model scenarios A3b and E0b was smaller than that in scenarios A3a and E0a (Fig. 9). The largest reduction in parameter uncertainty in scenarios A3b and E0b compared with A3a and E0a was in the fishing mortality and catchability parameters; uncertainty in other parameters was similar when comparing these scenarios (results not shown).

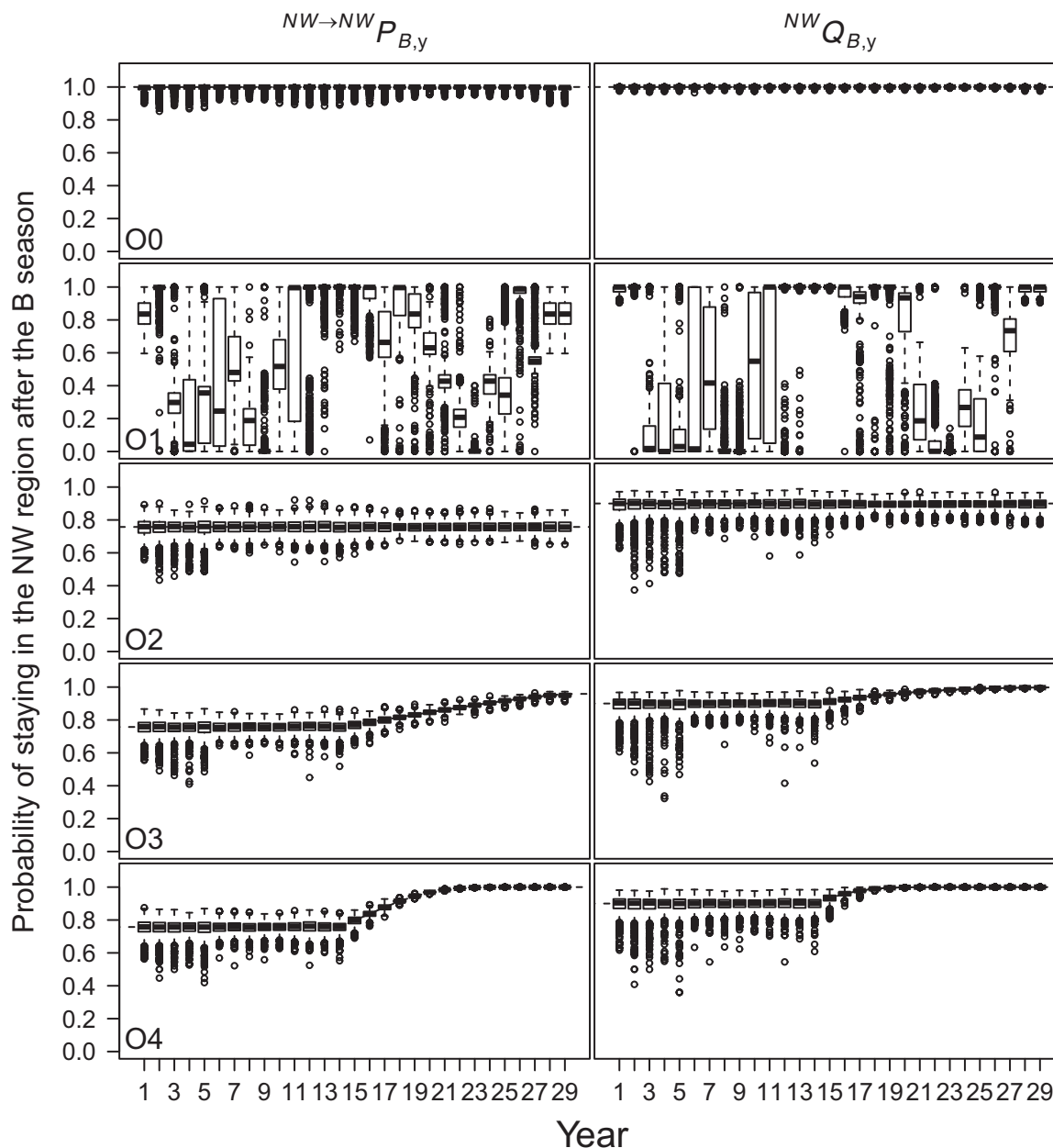
Discussion

In this study we have illustrated cases in which a spatially explicit ASA model that includes movement in population dynamics

is both superior and inferior to the commonly used spatially aggregated ASA model. In particular, when movement was random between regions, spatially aggregated model scenarios produced unbiased total biomass estimates, but spatially explicit model scenarios produced biased total and regional biomass estimates and highly uncertain movement parameters. Alternatively, there were several spatially explicit models that produced unbiased estimates of total and regional biomass under climate-forcing scenarios, while spatially aggregated estimation models were biased. Specifically, the spatially aggregated estimation model with constant fishing selectivity over time failed to account for differences in age-specific full-recruitment fishing mortality between areas and (or) gears. In general, the primary advantage shown in this analysis of a spatially explicit ASA model compared with a spatially aggregated ASA model is the potential reduction of uncertainty in biomass estimates.

For each of the operating model cases investigated in this study, the resulting error in model estimates was larger in the spatially

Fig. 6. Movement ($^{NW \rightarrow NW}P_{B,y}$) and ontogenetic ($^{NW}Q_{B,y}$) time-dependent parameter estimates from estimation model E4. Parameters for the northwest (NW) region after the B fishing season are shown as an example; the dashed lines are the values from the operating model (omitted for case O1, as movement was random).



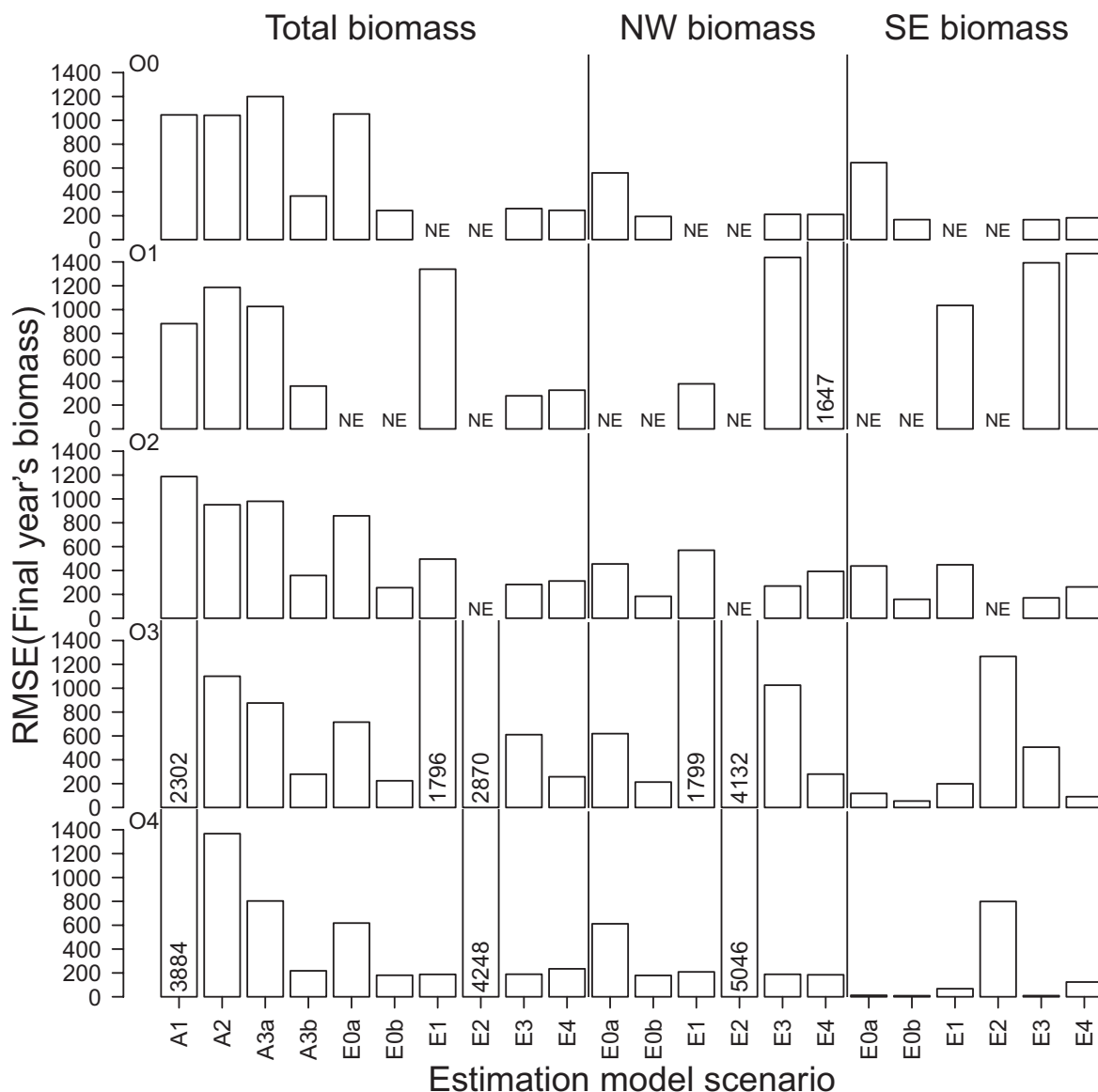
aggregated estimation model scenarios compared with that in the spatially explicit estimation model scenarios. This general result is somewhat surprising because of the larger annual sample sizes in the aggregated data compared with sizes in the spatially explicit data; the variance in the datasets fitted by the spatially aggregated model was smaller than the variance in the datasets fitted by the spatially explicit model. We discovered that the primary reasons for reduced uncertainty in the spatially explicit estimation model scenarios was because of a better accounting of underlying processes (e.g., changes in parameter values over time or space). However, the inclusion of tagging data in both the spatially aggregated and spatially explicit estimation models greatly reduced uncertainty.

This resulting reduction of uncertainty in the estimation model scenarios using tagging data was due to a gain in precision of the fully recruited fishing mortality parameter estimates. This gain in

precision occurred in the fishing mortality for both the spatially aggregated and spatially explicit estimation model scenarios. As might be expected, reduced uncertainty in the fishing mortality rates was accompanied by increased precision of the catchability parameters for the survey indices (because fishing rate estimation precision is correlated with precision in abundance estimates). Further, the addition of tagging data had little effect on the uncertainty in the movement parameters in the spatially explicit estimation model. While the spatially explicit estimation model did have lower uncertainty than the aggregated model, when tagging data were included in the spatially aggregated model the uncertainty in biomass and parameters were comparable to the uncertainty from the more complex spatially explicit estimation model.

Causes of process error in spatially aggregated datasets can include time-varying changes in the spatial distribution of the pop-

Fig. 7. Root mean squared error (RMSE) in total and regional biomass estimated in the final year from the estimation model scenarios. "NE" stands for estimation model scenarios that were not estimated in the specific operating model case.



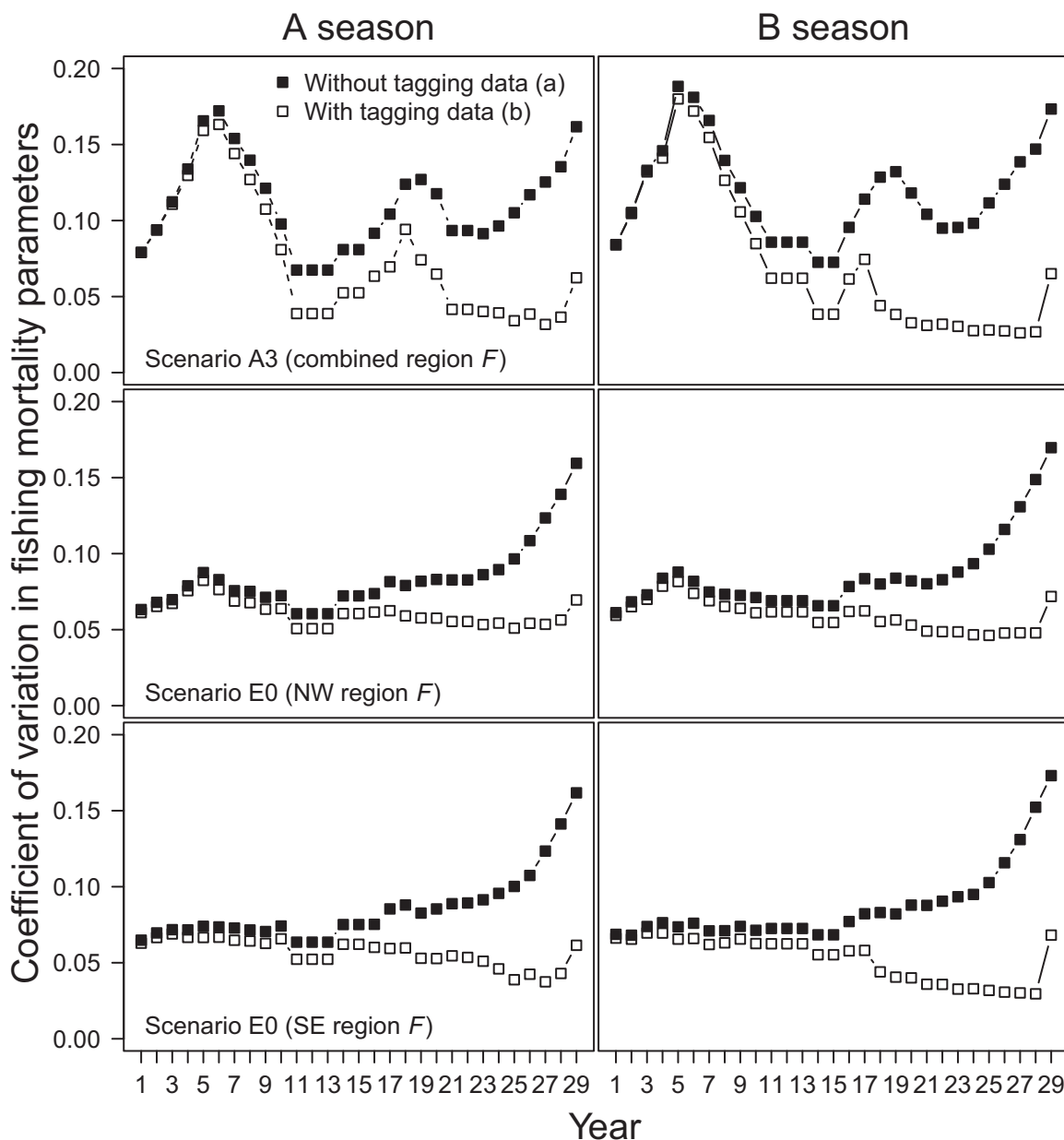
ulation, fishing gear selectivity, and full-recruitment fishing mortality (Sampson and Scott 2011). In this study, the operating model was specified to have the same fishery selectivity between areas over time; however, there were spatial differences in the annual distribution of the population and full-recruitment fishing mortality. The effect of aggregating catch data across regions (catch biomass and catch-at-age) resulted in fishing mortality that varied by both time and age. Sampson and Scott (2011) noted in a similar situation that fishing mortality with increasing age can become dome-shaped and vary over time. In this study, after aggregating spatially explicit catch data, dome-shaped and time-varying fishing mortality also occurred and further did not necessarily follow easily parameterized functional forms.

The spatially aggregated models with constant selectivity over time failed to account for this type of process error. This resulted in larger errors when compared with the spatially explicit model and also caused small biases. Two estimation scenarios tested in this study reduced bias. In the first it was shown that use of the Dirichlet to estimate the effective sample size for the age composition data reduced bias in the spatially aggregated model. This

was because the aggregated fishing mortality rates across ages induced overdispersion in the fishery age composition data when constant selectivity over time was assumed in the estimation model. However, the problem of assuming constant and separable selectivity remained. The second scenario estimated nonparametric selectivity that was time dependent, resulting in the ability to correctly estimate the true underlying aggregated fishing mortality from the operating model. Comparing the two alternatives, when movement was constant, random, or did not have climate change effects, estimating effective sample size performed just as well and better in some cases than nonparametric selectivity in terms of RMSE in biomass. Although, when climate change induced a distributional shift, the RMSE in biomass from nonparametric selectivity was smaller than when estimating effective sample size. Such a pattern would support the approach used in the Ianelli et al. (2011b) assessment, which estimates nonparametric and time-varying selectivity.

When bias in estimates of total and regional biomass was present in the spatially explicit ASA model, it occurred when movement between regions was random and when the ontogenetic and

Fig. 8. Coefficient of variation in fishing mortality from estimation model scenarios A3a and A3b (combined region F) and E0a and E0b (NW and SE region F) for the A and B fishing seasons.

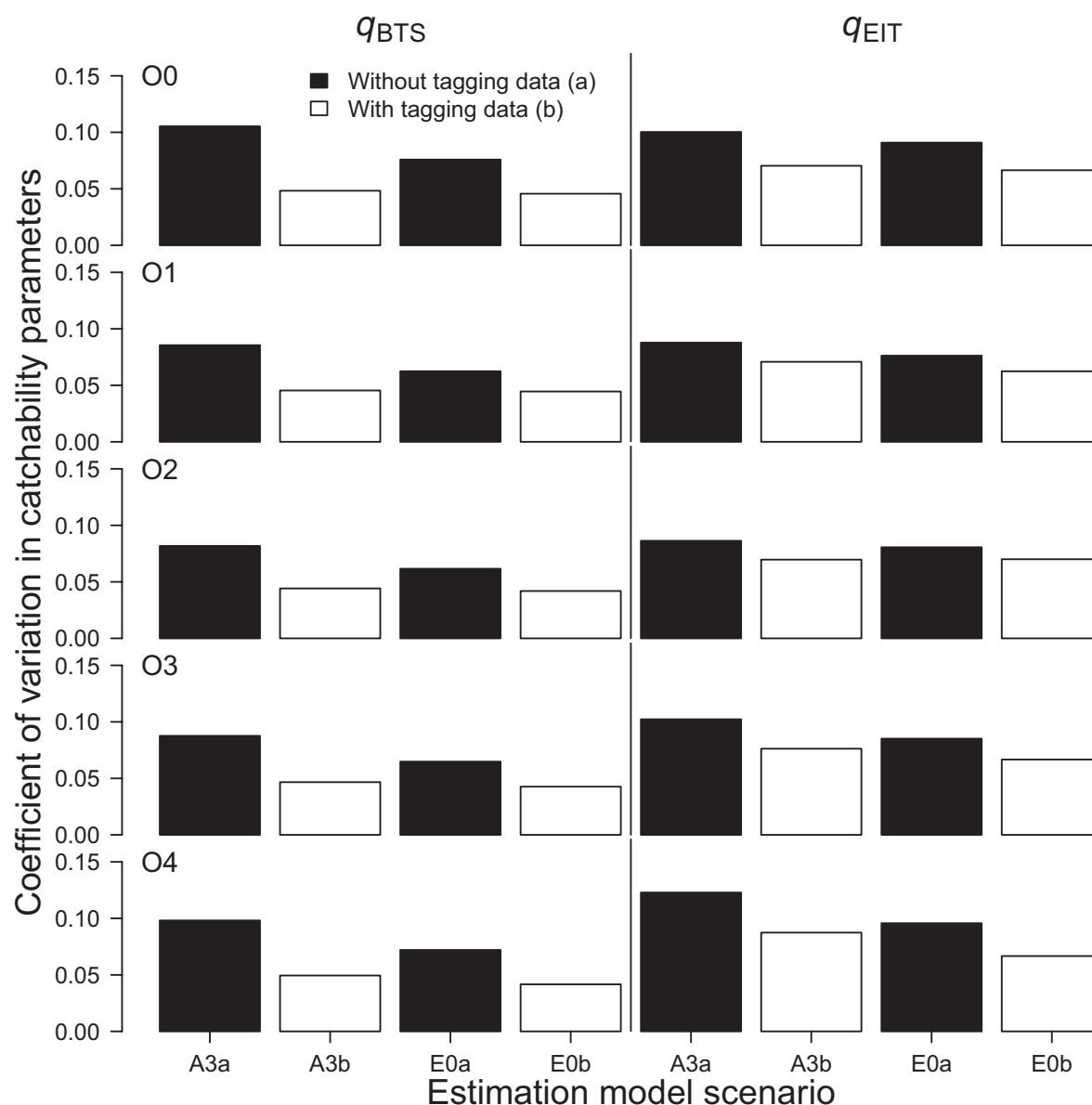


climate change parameters were misspecified. The biased biomass in both estimation model scenarios (E1 and E2) was due to the failure of the model to detect a northward shift in the population. In performing stock assessment this bias could be identified through the fit to regional index data (i.e., catch or survey biomass), as the fit to each region's index data degraded as climate change forcing shifted the population northward. In terms of management, bias in total and regional biomass would result in suboptimal spatial allocation of catch with overexploitation in one region and underexploitation in the other. If ontogenetic effects are unknown, bias in stock assessment and incorrect management actions could result (Lindeman et al. 2000). We extend this concept by showing that the same is true for climate change forcing, and the bias when time-dependent changes in movement are unaccounted for can be greater than misspecifying ontogenetic movement. We have shown that if ontogenetic movement or climate change effects causing time-dependent movement are

misspecified, a spatially explicit model might provide little benefit over simpler spatially aggregated models.

With the addition of tagging data in the spatially explicit models (including the random walk estimation model), it was possible to estimate time-dependent changes in ontogenetic movement. Random walks have often been used to estimate time-dependent deviations in parameter estimates (e.g., Wilberg and Bence 2006). However, a drawback of this approach is the potential for the number of parameters estimated to increase considerably. For example, there would be an increase of $Y - 1$ parameters (where Y is the total number of years modeled) if a random walk is applied to estimate time-dependent deviations in a given parameter; the same reasoning would apply if estimating parameter deviations by age, sex, region, etc. In this study we found that a scaled random walk could be used to reduce the number of parameters estimated where a single vector of shared annual deviations was estimated and applied to a number of parameters by multiplying

Fig. 9. Coefficient of variation in catchability of the bottom trawl survey (BTS) and echo-integration trawl survey (EIT) from estimation model scenarios A3a, A3b, E0a, and E0b.



the shared deviation by the parameter's initial value estimate. However, this requires a strong and possibly incorrect assumption that whatever the mechanism (e.g., temperature, food availability, etc.) causing time-dependent changes, it would affect each parameter similarly.

There were a number of simplifying assumptions made in specifying the operating and estimation models used in this study. One simplifying assumption in this study was that the spatial scale used in the operating model was the same as the estimation models (where relevant). An operating model with finer spatial scales than the estimation model is likely to result in increased errors in full-recruitment fishing mortality estimates. Another simplifying assumption was that in the estimation models that included tagging data, the age at the time of release was assumed to be known, which would not be the case in real-world applications. Further, catchability and survey selectivity were assumed to be time-invariant. The limitations of a spatially explicit ASA model in real-world situations would depend on the amount and quality of available spatially explicit data.

Both the spatially aggregated and spatially explicit ASA models have drawbacks and advantages (e.g., Quinn and Collie 2005). A primary drawback of the spatially aggregated model is the inability to estimate regional biomass. In terms of management, it could become difficult to properly manage fishing effort with a spatially aggregated model if climate change were to induce a northward shift in fish populations (Cheung et al. 2009). An advantage of a spatially aggregated ASA model is that accurate estimation of total biomass can be obtained without having to know or parameterize ontogenetic or climate change parameters for movement. A drawback of the spatially explicit model is potential model specification error when considering ontogenetic (Elsdon and Gillanders 2003) or climate change effects on movement or recruitment. Further, a limitation of implementing spatially explicit ASA models is the magnitude of the regional sample sizes in the datasets (e.g., population index data and age composition). Often, sample sizes within regions are too small to support reliable estimation using a spatially explicit model. Thus, reduction of uncertainty in estimates of biomass through the use of a spa-

tially explicit model in this case is unlikely. When data are adequate, advantages of the spatially explicit model include the ability to estimate regional biomass and may lead to increased precision in total biomass. Management implications would become more important given recent work on accounting for uncertainty when setting harvest recommendations (e.g., [National Research Council 1998](#); [Prager and Shertzer 2010](#)).

We have shown that under certain circumstances a spatially explicit ASA model provides the ability to identify potential effects on fish population dynamics by climate change and adjust management of commercial fisheries based on changes in the spatial distribution of fish species. We also have shown cases in which a spatially explicit model fails to provide improvements over a spatially aggregated model, in particular when movement is random and when ontogenetic or time-dependent changes in movement are incorrectly specified. As an intermediate step to ecosystem-based fisheries management, we recommend that spatially explicit models continue to be developed and that tagging programs be implemented. Tag recovery data would help identify changes in fish spatial distribution due to climate change and also better estimate fishing mortality at a finer scale. With the addition of tagging data, the reduced uncertainty in both a spatially aggregated and spatially explicit models would better inform management decisions on size and allocation of catch quotas, even if the spatial distribution were affected by climate change. Further, with proposed methods to incorporate uncertainty in harvest recommendations (i.e., [Prager and Shertzer 2010](#)), the larger uncertainty in a model without tagging data would result in catch limits that are smaller than the ones obtained from a more precise model that included tagging data. Using this type of method to derive catch limits could potentially offset some costs associated with implementing tagging programs that aid in reducing uncertainty in stock assessment models.

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